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Stabilimenta attract unwelcome predators to orb-webs

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Conspicuous behaviour exposes animals to predation; prey-attraction thus often conflicts with antipredator behaviour. The fact that a conspicuous ultraviolet-light reflecting silken structure in the orb-webs of certain spider species, known as a stabilimentum, makes the webs obvious to both prey and predators has been used to argue that spiders benefit from building stabilimenta by attracting prey and/or defending against visually hunting predators. Here, we provide experimental evidence that stabilimenta can act as visual signals that attract web-invading spider-eating predators with acute vision to the webs. We also show that the predators can learn to remember a particular type of stabilimentum. Thus, stabilimentum-building spiders risk a high level of predation by attracting visually hunting predators.

Keywords: *Argiope versicolor*; silk; stabilimenta; spider; *Portia labiata*; predator attraction

1. INTRODUCTION

Biologists have always been fascinated by the spider's web in all its various forms (see Foelix 1996) and long been puzzled by the function of the so-called stabilimenta in the webs of certain orb-weaving spiders (Robinson & Robinson 1970). The orb-web is well known as a device used in foraging as well as in defending against predators (e.g. Tolbert 1975; Edmunds & Edmunds 1986; Eberhard 1990; Blackledge & Wenzel 1999). The stabilimentum, however, is an extra silk structure that is added by certain species of spider to the central portion of the orb-web after web construction. Why these spiders, but not others, include stabilimenta in their webs has been debated for more than a century (Simon 1895). Although many functional hypotheses have been proposed for silk stabilimenta, the most recent and plausible, but also contentious, hypotheses are the prey-attraction hypothesis (Craig & Bernard 1990; Elgar *et al.* 1996; Tso 1996, 1998; Watanabe 1999) and the predator-defence hypothesis (Horton 1980; Eisner & Nowicki 1983; Schoener & Spiller 1992; Kerr 1993; Blackledge 1998*a*; Blackledge & Wenzel 1999). Interestingly, both hypotheses have used the fact that stabilimenta have a bright reflectance across wavelengths of light visible to some animals, including ultraviolet (UV) light (Craig & Bernard 1990), to argue that stabilimenta act as visual signals that make webs more conspicuous either to prey or to predators. Thus, spiders benefit from building conspicuous stabilimenta by attracting prey to the webs, by advertising the presence of sticky webs to predators or by distracting predators. However, building stabilimenta may be costly because stabilimenta provide visual cues that insect prey use to avoid webs, thus reducing the web builder's foraging efficiency (Blackledge 1998*a*; Blackledge & Wenzel 2000, 2001). However, predators can also potentially perceive these conspicuous visual signals. Therefore, one may hypothesize that the stabilimenta could also operate to the detriment of a spider by attracting unwelcome visual predators to the orb-web, if UV-reflecting stabilimenta make webs more conspicuous. Surprisingly, no effort has been made to test this hypothesis. Here, we experimentally test this hypothesis using a species of orb-web weaving spider, *Argiope versicolor* (Doleschall) (Araneae: Araneidae), and a species of predator, *Portia labiata* (Thorell), a web-invading and spider-eating jumping spider (Araneae: Salticidae) from Singapore.

Like other *Argiope* species, *A. versicolor* build different types of stabilimenta, including disc-like stabilimenta built only by juveniles and cruciforms created by adults. A total of five different types of stabilimenta have been described in *A. versicolor* (figure 1; W. K. Seah and D. Li, unpublished data). It is known that webs with stabilimenta are able to attract prey (Craig & Bernard 1990; Tso 1996, 1998; Watanabe 1999; but see Blackledge & Wenzel 1999). As mentioned above, conspicuous signals may also attract the attention of predators (Eisner & Nowicki 1983). *P. labiata* is sympatric with *A. versicolor* and is known to enter the webs of *A. versicolor* to prey on it, both in nature and in the laboratory (D. Li, unpublished data). Like other salticids, *Portia* spp. differ from most spiders in having remarkably acute vision (Blest *et al.* 1990) that permits them to discriminate visually between different prey, predators and conspecifics (Jackson & Blest 1982; Li & Jackson 1996). Jumping spiders are also known to be dichromatic, having the physiological capacity to distinguish colours using the UV-sensitive and green-sensitive cells in their principal (anterior median) eyes (Land 1969; DeVoe 1975; Nakamura & Yamashita 2000). On the basis of visual cues alone, *Portia* spp. can distinguish a web from an empty cage, and can also distinguish between quiescent spiders, insects and egg sacs (Jackson 1995; Jackson & Pollard 1996; Li & Jackson 1996). Therefore, we assume that *P. labiata* is able to distinguish between decorated and undecorated webs and that it can make a choice as to which web it wants to enter.

In this study, we use *P. labiata* as a predator of *A. versicolor* to test three hypotheses: first, that *P. labiata* can use conspicuous UV-light reflecting stabilimenta to locate and catch *A. versicolor*; second, that the presence of *A. versicolor* has no effect on the attraction of *P. labiata* by

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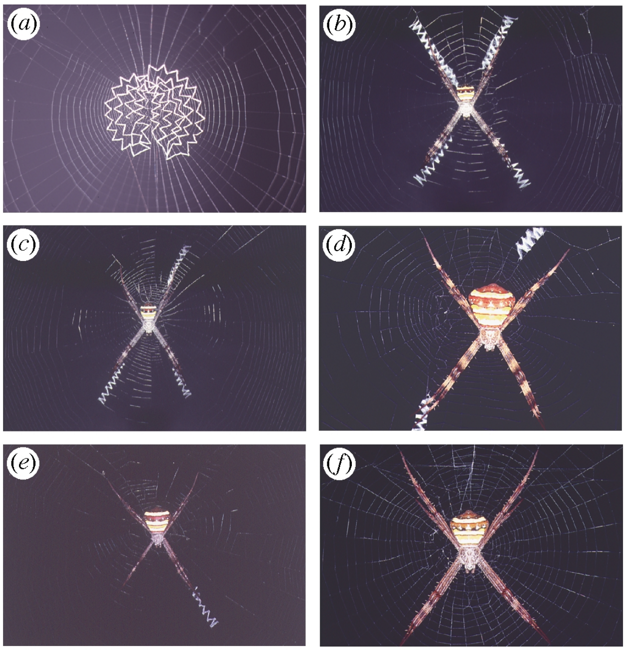


Figure 1. Webs and forms of stabilimenta of *Argiope versicolor*. The spiders either spin a new decoration each day, which may vary in design, or do not decorate their webs at all. (*a*) Disk-like (discoid) stabilimentum built by juveniles, (*b–e*) cruciform stabilimenta with four, three, two and one arms, respectively, and (*f*) a web without a stabilimentum. Scale bar: *ca.* 1 cm.

stabilimenta; and third, like stingless bees that can learn to avoid webs (Craig 1994), *P. labiata* is able to remember a particular type of decorated web.

2. METHODS

(a) General

Maintenance procedures, cage design, basic testing methods and terminology were as reported in earlier spider studies (see Jackson & Hallas 1986) and only essential details are given here. All experiments were carried out in a controlled laboratory (relative humidity, 80–90%; temperature, 24 ± 1 °C; 12 L:12 D photoperiod; laboratory light intensity, 332.8 ± 4.3 lux).

We collected *A. versicolor* juveniles and females from Bukit Timah Nature Reserve in Singapore in 1999. They were kept individually in plastic-framed cages with removable glass sides (200 mm × 200 mm × 50 mm). Wooden sticks were connected to the sides of the cages to provide attachment sites for the webs. *A. versicolor* fastens web lines primarily to the wooden sticks and the plastic frame instead of to the glass, and so the sides could be removed from the cages with minimal damage to the webs. Except when otherwise stated, the webs were always exposed during the tests to ensure that the predator, *P. labiata*, could see the web without obstruction or reflection from the cage. *A. versicolor* juveniles were used to build discoid stabilimenta and *A. versicolor* adult females were used to build cruciform stabilimenta with different numbers of arms (see figure 1). Both vacant webs (i.e. *A. versicolor* was not on its web) and webs with *A. versicolor* were used. Vacant webs were obtained by removing the host spiders 24 h before tests began.

We used laboratory cultures of *P. labiata* that originated from specimens collected in the habitat of *A. versicolor*. All *P. labiata* used were females (body length, 6–8 mm) that did not have any experience of *A. versicolor* prior to testing. They were kept individually in plastic cylindrical cages (diameter × height: 100 mm × 80 mm) and provided with a diet of fruit flies (*Drosophila melanogaster* Meigen) and houseflies (*Musca domestica* L.) *ad libitum* before testing. No individual *P. labiata* was used in more than one test of any one type.

(b) *Predator-attraction test*

We designed a choice test to determine whether *P. labiata* could be attracted to a web by the presence of a stabilimentum. A web without a stabilimentum (figure 1*f*) was compared with one with a stabilimentum (figure 1*a–e*), making an effort to pair similarly sized webs. Each *P. labiata* was starved for 1 week before the test. We conducted two series of tests: in one series, *P. labiata* were tested using webs with *A. versicolor* left in them; in the other series, the same *P. labiata* were tested using webs without *A. versicolor*. Testing began by putting *P. labiata* between two cages that bore webs. The two webs were set 20 cm apart and *P. labiata* was placed 10 cm from each web. Each test ended when *P. labiata* chose one of the two webs in the vacant-web tests, ate one *A. versicolor* in the occupied-web tests or when 10 min had elapsed, whichever came first. However, observations were continued until the sequence had terminated if *P. labiata* responded to a web, even after the allocated time. All tests were conducted in a plastic box with a glass bottom. After each test the glass panel was wiped with 70% ethanol and with distilled water to ensure that all secretions and pheromones deposited by the previous *P. labiata* were removed. We ran all tests under the same light conditions (light intensity, 430.2 ± 17.40 lux) and a sheet of black cardboard was provided as a background for each web. We analysed the data using a χ^2 test of goodness of fit (Zar 1996).

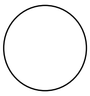
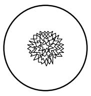
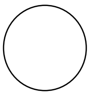
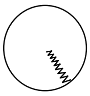
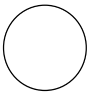
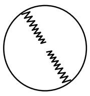
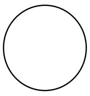
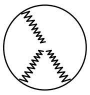
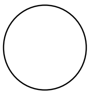
(c) *Effect of* A. versicolor *on attraction of predators to webs*

A. versicolor may be attractive to predators, so the presence of a spider may affect the attraction of predators to the web. To test the influence of *A. versicolor*, a naive *P. labiata* was given a choice between webs with and without *A. versicolor*, making an effort to pair similarly sized webs with the same type of stabilimentum. Testing began by putting a *P. labiata* between two web-bearing cages as in the predator-attraction tests. Tests ended when *P. labiata* chose one of the two webs or when 10 min had elapsed, whichever came first. Comparisons were made using the χ^2 test of goodness of fit (Zar 1996).

(d) *Learning experiments*

Portia spp. are known to exhibit trial-and-error learning (Jackson 1992; Jackson & Wilcox 1993). To examine the ability of *P. labiata* to detect and remember webs with stabilimenta, we individually trained *P. labiata* to associate decorations with foraging success. *P. labiata* was first trained to associate the cruciform stabilimentum with one arm in the web with food, *A. versicolor*. Then, a web with a one-arm cruciform stabilimentum was used in combination with a web with any other type of stabilimentum. The two webs were presented to *P. labiata* simultaneously, but *A. versicolor* was only present in the hub of the web with the one-arm cruciform stabilimentum. In the other web, a small piece of cotton ball was attached on the hub to replace the absent prey. *P. labiata* was starved for 3 days before the experiments. Each *P. labiata* was allowed to take its time to find the web containing the food. Those that went to the web with the cotton ball were gently removed back to the starting point, and the training continued until they got onto the web with the

Table 1. Results from predator-attraction tests in which one web with stabilimentum and one web without a stabilimentum were presented to *Portia labiata* simultaneously in bright conditions (430.2 ± 17.4 lux).

web A	web B	presence/absence of *A. versicolor*	number choosing web A first	number choosing web B first	test of goodness of fit
		present	13	27	$\chi^2 = 4.90$; $p < 0.05$
		absent	12	28	$\chi^2 = 6.40$; $p < 0.01$
		present	13	27	$\chi^2 = 4.90$; $p < 0.05$
		absent	12	28	$\chi^2 = 6.40$; $p < 0.01$
		present	8	32	$\chi^2 = 14.4$; $p < 0.001$
		absent	10	30	$\chi^2 = 10.0$; $p < 0.005$
		present	11	29	$\chi^2 = 8.10$; $p < 0.005$
		absent	8	32	$\chi^2 = 14.4$; $p < 0.001$
		present	9	31	$\chi^2 = 12.1$; $p < 0.001$
		absent	7	33	$\chi^2 = 15.7$; $p < 0.001$

one-arm cruciform stabilimentum. The training exercise was performed eight times, twice for each pair of web types, with each *P. labiata*. When *P. labiata* chose the right web, it was allowed to feed on *A. versicolor* for 5 min as a reward. Subsequently, the trained *P. labiata* were kept without food for 3 days after the date of learning. They were then used in the learning experiments to determine whether they could associate a stabilimentum with food. We also used a choice test to examine whether a predator remembered the familiar stabilimentum. In these tests, two webs, one with a familiar stabilimentum (one-arm cruciform) and the other with an unfamiliar stabilimentum, had *A. versicolor* present in the centre of the hub. Each test began by putting a trained *P. labiata* in between the two webs, as in the predator-attraction tests. Tests ended when *P. labiata* chose one of the two cages and entered the web or when 10 min had elapsed, whichever came first.

3. RESULTS

(a) *Predator-attraction test*

When given a choice between webs with and without stabilimenta, regardless of whether *A. versicolor* was in the web or not, *P. labiata* preferred the webs with stabilimenta to those without stabilimenta in all tests on all five combinations of webs (table 1).

(b) *Effect of the presence of* A. versicolor *on the attractiveness of webs to predators*

When given a choice between webs with and without *A. versicolor*, *P. labiata* chose the webs with *A. versicolor* as often as they chose the webs without *A. versicolor* (table 2).

(c) *Learning experiments*

When *P. labiata* were trained to associate a one-arm cruciform stabilimentum with the presence of *A. versicolor*, *P. labiata* chose the web with the one-arm cruciform (familiar) stabilimentum more often than they chose other types of decorated webs (table 3).

4. DISCUSSION

When a predator (receiver) encounters a spider (sender) in a web with a conspicuous UV-reflecting stabilimentum (visual signal), there are three possible responses: first, being trapped if the predator is unable to determine the presence of the stabilimentum in the web; second, avoiding the web passively or actively (e.g. some arthropod predators and birds); and third, being attracted to the web if it is able to see the stabilimentum. Surprisingly, almost all studies investigating the adaptive significance of stabilimenta as defensive structures have tried to examine how a predator avoids a web with a stabilimentum (e.g. Blackledge 1998*a*; Blackledge & Wenzel 1999, 2000). Horton (1980) stated that the web is a negative stimulus to a bird because sticky silk adheres to the bird's feathers and clumps them; Horton found that the cross (cruciform) stabilimentum advertises the presence of the noxious web, enabling birds to avoid webs with stabilimenta. Eisner & Nowicki (1983) measured the durability of 30 webs with stabilimenta and 30 webs without stabilimenta in the field, and found that 8% of the stabilimentum-free webs persisted undamaged as compared with 60% of the webs with

Table 2. Results from tests of the effect of the presence or absence of *Argiope versicolor* on the attraction of predators to webs. A naive *Portia labiata* was given a choice between a web with *A. versicolor* left in it and a web without *A. versicolor*; both webs had with the same type of stabilimentum.

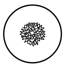
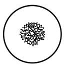
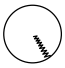
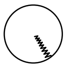
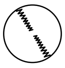
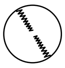
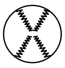
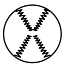
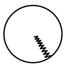
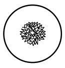
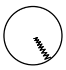
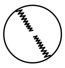
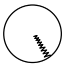
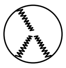
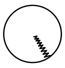
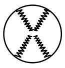
web (A), with *A. versicolor*	web (B), without *A. versicolor*	number choosing web (A) first	number choosing web (B) first	test of goodness of fit
		16	14	$\chi^2=0.133$, not significant
		17	13	$\chi^2=0.533$, not significant
		18	12	$\chi^2=1.2$, not significant
		17	13	$\chi^2=0.533$, not significant
		18	12	$\chi^2=1.2$, not significant

Table 3. Results from learning experiments in which a *Portia labiata* trained with a one-arm cruciform stabilimentum plus food as a reward was given a choice between a web with a familiar stabilimentum (one-arm cruciform) and a web with an unfamiliar stabilimentum; both webs contained *Argiope versicolor*.

(Data in the third and fourth columns only are used in these tests. Null hypothesis: if *P. labiata* chose a web, then the probability of choosing web A, with a familiar stabilimentum, is equal to the probability of choosing web B, with an unfamiliar stabilimentum.)

web A	web B	number choosing web A first	number choosing web B first	test of goodness of fit
		26	12	$\chi^2=5.16$; $p<0.05$
		27	14	$\chi^2=4.10$; $p<0.05$
		29	11	$\chi^2=8.10$; $p<0.005$
		30	9	$\chi^2=11.3$; $p<0.001$

stabilimenta. Thus, 'web durability was therefore due to the presence of the visual markers' and 'stabilimenta serve as visual advertisements of webs' (Eisner & Nowicki 1983, p. 186). Blackledge & Wenzel (1999) conducted experiments to determine the effect of stabilimenta on web damage by birds, and their data support the hypothesis that stabilimenta can function as a defence against birds.

In this study, we have demonstrated experimentally that predators are attracted to webs by the stabilimenta and feed on the resident spiders: the web-invading spider-eating jumping spider *P. labiata* consistently chose the webs with stabilimenta more often than the webs without stabilimenta (table 1). We also found that the presence of *A. versicolor* in the web had no effect on *P. labiata*'s attraction to the stabilimenta (table 2). Our results suggest that the stabilimenta alone is a sufficient visual signal to attract predators to the web. Not surprisingly, stabilimenta acting as highly visual signals to prey and predators create trade-offs in signal design between foraging, avoiding attack by predators and defence when actually attacked. Like other visual signals that are designed for communicating with conspecifics that carry a greater risk of predator attraction (Guilford 1990; Endler 1993; Ryan & Rand 1993), conspicuous stabilimenta built by the orb owners to attract visual prey or to warn some visual predators of the presence of noxious sticky silk in the orb-webs may also increase the risk of predation by attracting particular types of predators.

However, whether or not the silk is conspicuous to insects is controversial and has important implications for the function of stabilimenta (in terms of the prey-attraction hypothesis versus the predator-defence hypothesis) (Craig & Bernard 1990; Blackledge 1998*a*; Blackledge & Wenzel 1999, 2000). The prey-attraction hypothesis argues that UV reflection makes stabilimenta conspicuous to insects and attracts insects to webs (Craig & Bernard 1990; Tso 1996, 1998; Watanabe 1999; Herberstein *et al*. 2000). However, the predator-defence hypothesis suggests that insects avoid webs, based upon the presence of stabilimenta, and that reflection of UV light is crucial to make the stabilimenta cryptic to insects, thereby reducing their ability to avoid webs (Blackledge 1998*a*; Blackledge & Wenzel 2000, 2001). There are several explanations for the incompatible differences between these two hypotheses. Many of the data relating to the attraction of prey to stabilimenta are correlational (Craig & Bernard 1990; Tso 1996, 1998; Watanabe 1999; Herberstein *et al*. 2000), while the data supporting insect avoidance of stabilimenta come from a manipulative experiment (Blackledge & Wenzel 1999) that controlled for a strong influence of foraging success on the presence of stabilimenta in webs. Several studies have shown that spiders capturing more prey are more likely to build stabilimenta, which can produce a correlation between the capture of high numbers of prey and the presence of stabilimenta in webs (Blackledge 1998*b*; Herberstein *et al*. 2000). Furthermore, choice experiments demonstrating attraction of insects to stabilimenta have been performed in laboratory settings (Craig & Bernard 1990; Watanabe 1999), while the choice experiment showing the cryptic nature of the silk to bees was performed under natural conditions (Blackledge & Wenzel 2000). The background against which a signal is viewed is crucial to its conspicuousness (Blackledge 1998*a*). Animals can easily find a signal conspicuous in the laboratory when that same signal is inconspicuous outside. We have demonstrated that *P. labiata* are capable of using stabilimenta to locate *A. versicolor* prey in the laboratory, but it remains to be determined how important this is for *P. labiata* in the field.

If a web-building spider consistently builds the same form of stabilimentum in its web, it may increase the risk of predation because predators may remember the form of the stabilimentum. In the learning experiments, we demonstrated that *P. labiata* can learn to associate the form of the stabilimentum with food: when given a choice between a web with a familiar form of stabilimentum and a web with an unfamiliar form of stabilimentum, *P. labiata* chose to enter the web with the familiar form of stabilimentum more often than the web with the unfamiliar form of stabilimentum.

Building stabilimenta may attract more prey, thus increasing foraging efficiency (Craig & Bernard 1990; Elgar *et al*. 1996; Tso 1996, 1998; Watanabe 1999), or reduce the risk of predation (Robinson & Robinson 1970; Eisner & Nowicki 1983; Blackledge 1998*a*,*b*; Blackledge & Wenzel 1999). To increase their foraging success by building stabilimenta to attract prey and, at the same time, reduce the risk of predation, spiders must have strategies to balance the trade-off. Variation in stabilimentum-building behaviour seems to be a strategy that has evolved in these spiders to balance this trade-off. In nature, when *Argiope argentata* spins a new web each morning the spider produces a decoration whose pattern or pattern orientation differs from that spun the previous day, and on some days spiders spin no decoration at all (Craig 1994). By varying their web decorations randomly and daily, *A. argentata* seem to have evolved a foraging behaviour that inhibits bees both from learning to avoid webs and from remembering their location (Craig 1994) because learning is constrained by anatomical and physiological limits to the animal's perceptual capabilities and by the complexity of its neural-processing system (Dukas 1993; Bélisle & Cresswell 1997; Endler & Basolo 1998). Whether, by varying their web decorations randomly and daily, *Argiope* spiders also prevent some predators, such as *Portia*, from learning to be attracted to their webs needs further study.

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